

OBSERVATIONS ON SOME UPPER AMAZONIAN FORMICARIAL MELASTOMATACEAE

TREVOR WHIFFIN

Department of Botany, University of Texas, Austin, Texas 78712.

The observations reported here were made in the area around Leticia, Amazonas, Colombia during July and August 1968, and have subsequently been extended by further study in the herbarium. Nevertheless, apart from the section on taxonomic notes, the main emphasis is on the field observations, and the extent to which they support (or not) some current ideas related to formicaria and to speciation in the tropical rain forest.

The author citations for all names used in the first two sections of the paper (unless given) are provided in the section on taxonomic notes. Specimens collected from the various populations studied in the field are listed at the end of the paper.

FORMICARIA

A large proportion of upper Amazonian melastomes have formicaria. Among these are *Maieta guianensis* var. *guianensis*, *M. guianensis* var. *leticiana*, *M. poeppigii*, *Ossaea bullifera*, *Tococa juruensis*, *T. ulei* and *T. aff. stephanotricha*, which were studied in the field. Quantitative observations of the disposition of formicaria on a number of plants were made for *M. guianensis* var. *leticiana*, *M. poeppigii*, *T. ulei*, and *T. aff. stephanotricha*, while qualitative observations were made for the other three taxa.

In *Maieta guianensis* (Fig. 2A,B) and *M. poeppigii* (Fig. 2C), the leaves of a pair are usually markedly unequal; the larger leaf has a well-developed formicarium, the smaller leaf not. The general habit of *Maieta* is illustrated in Fig. 1, showing the relative positions of the larger and smaller leaves of each pair, and the disposition of the formicaria. Rarely both leaves at a node are more or less equal, and in this case both have a formicarium. Also, the rare intermediate leaves have formicaria of correspondingly intermediate size. There is no significant difference between the two species.

In *Ossaea bullifera* (Fig. 2D), the leaves are usually unequal, the larger having a formicarium and the smaller not.

In *Tococa juruensis* (Fig. 2E), the leaves are more or less equal, both having a formicarium; occasionally one leaf of a pair will be smaller, and with a small or no formicarium.

In *Tococa ulei* (Fig. 2F), a young seedling, at the first few nodes, has only one or sometimes neither of a pair of leaves bearing a formicarium. In larger plants, the situation is variable, even on the same plant. The leaves are not markedly anisomorphic, but usually one leaf of a pair is slightly smaller. The larger leaf has a large well-developed formicarium; the opposite, and usually slightly smaller leaf, has either a small formi-



Fig. 1. General habit of *Maieta guianensis* var. *leticihana* (Whiffin 68). $\times\frac{1}{2}$.

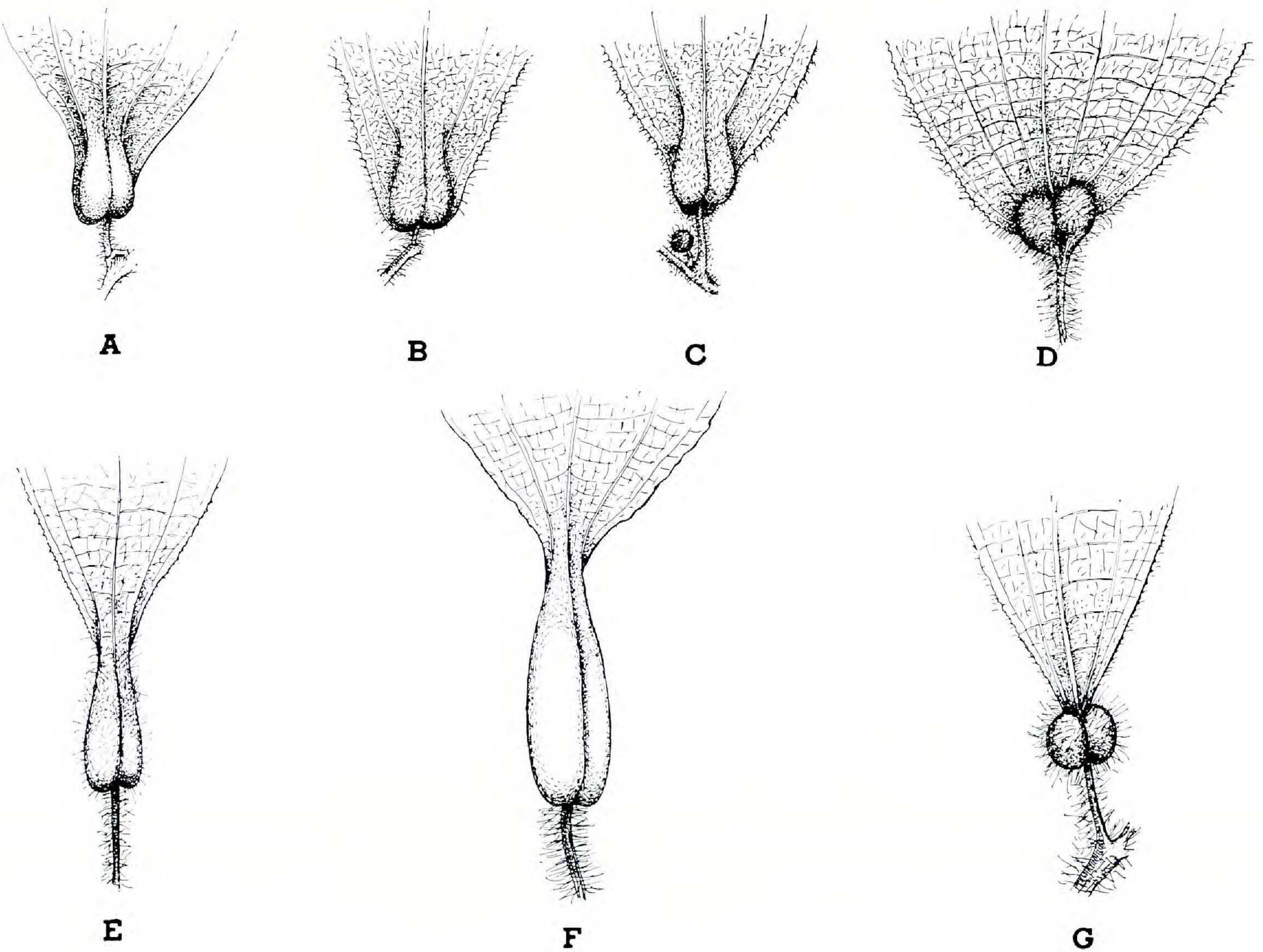


Fig. 2. Details of formicaria. A. *Maieta guianensis* var. *leticiana* (Whiffin 68); B. *M. guianensis* var. *guianensis* (Whiffin 21); C. *M. poeppigii* (Whiffin 56); D. *Ossaea bulifera* (Whiffin 18); E. *Tococa juruensis* (Whiffin 8); F. *T. ulei* (Whiffin 15); G. *T. aff. stephanotricha* (Whiffin 52). All $\times 1\frac{1}{2}$.

carium or none, in about equal frequencies. Occasionally this opposite leaf will have a large formicarium, and at other times a minute, scarcely developed formicarium. The disposition of these various forms on the mature plant seems to follow no set sequence. However, the size of the formicarium seems to vary proportionately with the size of the leaf (though not so markedly as in *Maieta*, where the range in leaf size is greater).

In an unidentified *Tococa* species (aff. *stephanotricha*) (Fig. 2G), the leaves at the lower two or three nodes are markedly unequal, with only the larger leaf of each pair having a formicarium; the leaves at higher nodes are more or less equal, and both have a subspherical formicarium.

The utility of the disposition of formicaria as taxonomic characters has not been extensively examined. Genera such as *Clidemia*, *Ossaea* and *Tococa* contain both formicarial and non-formicarial species; all three species of *Maieta* are formicarial. The formicaria appear to be a genetic feature, developing in *Tococa guianensis*, for example, even in the absence of ants (Wurdack, pers. comm.).

Observations on living plants indicate that the degree of development of the formicarium varies with the size of the leaf, as might be expected. Species which are markedly anisophyllous (e.g. in *Maieta*) have a formicarium usually only on the larger leaf of a pair, but if the opposing leaves are subequal to equal then both have a formicarium. Species in which the leaves are variably subequal to somewhat unequal (e.g. *Tococa ulei*) usually have a well-developed formicarium on the larger leaf, and an intermediate to no formicarium on the opposing leaf. Species in which the leaves are equal to subequal (e.g. *Tococa* aff. *stephanotricha*) usually have a well-developed formicarium on both leaves of a pair; often, however, there is some slight anisophylly even in these species, and the size of the formicarium will vary correspondingly. Any attempt to use disposition of formicaria as a taxonomic character would have to consider this problem of allometry.

The shape and probably also the placement of the formicaria is often, however, a useful taxonomic character. For example, the shape of the formicarium helps to distinguish *Tococa ulei* from *T. guianensis*; indeed, several *Tococa* species have formicaria with distinctive shapes.

There have been a number of observations on the function and evolution of formicaria (often also called myrmecodomatia). Various different types of relationship exist between ants and plants, as has been outlined by van der Pijl (1955). As regards formicarial melastomes, it appears that the plants provide shelter for the ants (a myrmecodomic relationship); there is no evidence that the plants provide a source of nutrition for the ants (Melin, 1931). It is often postulated that the ants protect the plant from attack by phytophagous insects; this proved to be so in bull-horn acacias, where the removal of the ant colonies was followed by severe defoliation of that acacia (Jansen, 1967). In addition, Jansen (1967, 1969) has noted an allelopathic effect of the ants, maintaining a cleared area

around *Acacia* and *Cecropia* by selectively killing the shoot and lateral branch tips of neighboring plants. However, there is no evidence of such an interaction between ants and formicarial melastomes. Melin (1931) could find no evidence that ants had any effect on the extent of leaf damage caused by phytophagous insects on several *Tococa* plants in middle Amazonia. Field observations in upper Amazonia would, on the whole, support Melin's conclusion. Although the question of allelopathy has not been investigated in formicarial melastomes, the advantage of this would be much less to melastomes growing as small shrubs in tropical rain forest than it is to *Acacia* and *Cecropia* trees in dense young secondary regrowth.

Spruce (1908) postulated a correlation between myrmecophily and inundation; this may have been due to the high frequency of *Cecropia* trees, which show myrmecophily, in the disturbed and often periodically inundated areas alongside the rivers. In the melastomes, however, there appears to be no such correlation. There are few melastomes in the várzea forest (periodically or seasonally inundated forest) and, although the latter are often, but not always, formicarial, there is also a high frequency of formicarial melastomes in the neighboring terra firme forest (upland). Melin (1931) also indicates that the formicarial melastomes which he studied were on the edge of the inundated areas, and in the terra firme forest.

As noted earlier, formicaria are probably produced even in the absence of ants; thus they are part of the genetic make-up of the taxon, and have presumably arisen and been fixed during the course of evolution. From the taxonomy of formicarial melastomes, it would appear that formicaria and the ant-plant relationship have arisen independently on a (small) number of separate occasions. Spruce (1908) attempted to explain this evolution in neo-Lamarckian terms; Melin (1931) could find no explanation in terms of selection as he could find no advantage to the plant from the relationship. At the moment, therefore, the question is not settled, at least in the melastomes. Some authors (Schnell, 1967, and others cited there) have indicated that formicaria may have arisen during evolution from acarodomatia, but the evidence at the moment is not very satisfactory. For selection to have favored the formation and evolution of formicaria, there must have been some selective advantage of the ants to the plant, even if the nature of this advantage is not known at present. Within the variation of the taxon, those forms which allowed or increased this association with ants would have been favored, thus facilitating the fixation of this trait in the population, and later in the taxon. This is similar to the idea of pre-adaptation (Jansen, 1966). A probable outline of the further development of the ant-plant relationship through co-evolution is well detailed by Jansen (1966).

SPECIATION

The modes of speciation in the tropics are probably not different in quality from those in temperate areas (Cain, 1969; Mayr, 1969), although

they may vary in the relative importance of the various different modes. Discussions of speciation in the tropics variously emphasize genetic drift in small populations (Federov, 1966) or natural selection (Ashton, 1969); sometimes other modes such as saltatory non-adaptive evolution (van Steenis, 1969) are postulated, but generally these are unsatisfactory.

The general assumptions concerning the rain forest environment are that it has been relatively stable over geological time, and that as far as plant survival is concerned, it is optimal, thus leading to the idea of a low survival level (van Steenis, 1969) and a consequent lack of selective force. The rain forest environment is complex, not only horizontally (area) but also vertically (different height levels). The greater diversity of niches is part, but probably not all, of the explanation for the greater diversity of species. Among the rain forest trees, especially those which are emergent or which form the canopy, fairly large, though comparatively widespread, populations occur which are probably interbreeding. Ashton (1969) has shown that selection appears to have been a factor in speciation in such trees. However, in understory shrubs, the populations in many cases appear to be rather small and isolated. Thus in the area around Leticia, only one small population of *Ossaea bullifera* and one of *Tococa juruensis* were found. Populations of *Maieta guianensis* var. *guianensis*, *M. guianensis* var. *leticiana*, and *M. poeppigii* were found more often, but each population consisted of one or, at most, a few individuals, and was some distance from any other population. Often, however, two or even all three taxa were found together, indicating a similar ecological preference, although no intermediates were found. The question of how these taxa diverged is less easy to answer. However, some insight may be gained from recent studies by Haffer (1969), indicating that the Amazonian rain forest has not remained stable over a long period of time. He presents evidence that, during the Pleistocene dry periods, rain forest vegetation was restricted to certain forest refugia, which probably corresponded with the present areas of higher rainfall; this theory is useful in explaining speciation and present distribution of Amazonian birds. His theory applies equally well to speciation in rain forest plants. *Maieta guianensis* var. *guianensis* and *M. poeppigii* are widespread across Amazonia; *M. neblinensis* is restricted to Cerro de Neblina, Amazonas, Venezuela, and presumably, after becoming isolated there, has diverged and become distinct. *M. guianensis* var. *leticiana* is found only in Amazonian Colombia and adjacent Perú and Brasil (Whiffin, 1971). Its distribution corresponds to the Napo forest refugium of Haffer (1969) or, perhaps more correctly, to the riverside refugia to the east of the main Napo refugium. This taxon could well have arisen in the forest refugium during one of the Pleistocene dry periods. A number of other melastomes have a very similar known distribution to *Maieta guianensis* var. *leticiana*; these include *Adelobotrys macrophylla* Pilger, *Clidemia ulei* Pilger, *Ossaea bullifera*, *Tococa juruensis*, and *Tococa ulei*.

TAXONOMIC NOTES

The notes given here refer specifically to those formicarial melastomes mentioned above, indicating a number of points of interest found while studying these taxa in the herbarium; notes on other melastomes collected are given by Whiffin (1970).

Maieta Aubl.

Maieta guianensis Aubl., which is widespread from the Guianas across Amazonia to eastern Colombia, Perú, Ecuador, and Bolivia, is fairly common in upper Amazonia. The variation in this latter area is greater than in other parts of its range, and proves to be of interest (Whiffin, 1971). Two varieties of *M. guianensis* are recognized: var. *guianensis* and var. *leticiana* Whiffin; both occur in the area around Leticia. *Maieta poeppigii* Mart. ex Triana is similarly widespread, though less commonly collected throughout its range. The two species are easily separated (Gleason, 1931a; Whiffin, 1971).

Ossaea bullifera (Pilger) Gleason.

This, a distinct species from a restricted area in upper Amazonia, has been very rarely collected. It may be recognized by the following characters: unequal leaves, the larger with a formicarium, the smaller not; young branches densely long-setose, and leaves long-setose on nerves, margin and formicarium, with long, white to golden, setae; inflorescence lax, sparsely long-setose, and hypanthium more densely long-setose, with some setae glandular; calyx lobes long and narrow, green; petals long and narrow, white to translucent; fruit a comparatively large, long-setose berry. This species, originally described in *Leandra*, was later transferred to *Ossaea* by Gleason (1931b); its lax, lateral or axillary inflorescence with a few four-merous flowers may be better placed in *Ossaea*, although its large, fleshy, blue fruit seems a little out of place.

Tococa juruensis Pilger.

This, one of the more easily recognized of the upper Amazonian species of *Tococa*, has only rarely been collected. It appears to have a distribution including upper Amazonian Brasil, Colombia and Perú. It may be recognized by the following characters: young branches, larger formicaria, peduncles, pedicels and hypanthia long-setose pubescent; leaves variously unequal to subequal, most having a formicarium of a size varying with the leaf size; hypanthium terete, the calyx more or less truncate.

Tococa ulei Pilger.

This species is common in the area around Leticia. It has sometimes been confused with *Tococa guianensis* Aubl., which has perhaps slowed down appreciation of its specific limits. *Tococa ulei* is an upper Amazonian species, mostly in Colombia, Perú, and adjacent Brasil.

The shape of the formicarium in *T. ulei* is variable; typically it is longer than broad, but sometimes it is aberrant and more or less hemispherical. The inflorescence is typically racemose, but may be a simple panicle.

Some collections of *T. ulei* may have been misidentified as *T. guianensis*,

which is usually paniculate but may also be racemose; in any case, there is no sharp distinction on this character. As presently understood, *T. guianensis* covers a wide undefined variation, and needs re-definition. Gleason (1931b) has some useful comments on this point. *T. ulei* is a distinct species, however, and may be separated from *T. guianensis* by the following characters: formicarium usually elongate on the larger leaves; leaves often elliptic, sometimes more elongate; hypanthium with ten broad veins; hypanthium at most sparsely hirsute, and usually scurfy or stellate pubescent to glabrous; calyx teeth with a terminal black bristle, which may be entire or divided into three (or rarely more).

Tococa ulei approaches, but is distinct from, the typical form of *T. bullifera* Mart. & Schrank ex DC.; however, some of the varieties placed under *T. bullifera* may be better considered as *T. ulei*. In some respects *T. ulei* is similar to *T. occidentalis* Naud., but is surely distinct; *T. occidentalis* is also similar to *T. guianensis*, but again they are probably distinct. In fact, *T. occidentalis*, a rather neglected species, appears to be somewhat intermediate between *T. guianensis* and *T. bullifera*, the latter in turn connecting with *T. ulei*.

Tococa ulei also approaches *T. discolor* Pilger, but in the latter the leaves are generally broader in shape, and less attenuate at the base. It is also similar to *T. loretensis* Ule, which does not have the black setae on the calyx lobes, but is otherwise very similar, especially in inflorescence form and hypanthium shape. These three upper Amazonian species, *T. discolor*, *T. loretensis*, and *T. ulei*, seem to form a very close group. It has not been possible to examine the types, but type photos are available. At the moment, no valid specific differences between the three can be found.

Tococa aff. *stephanotricha* Naud.

This plant, collected sterile, was not matched, but in vegetative details, especially pubescence, it shows affinities with *Tococa stephanotricha* Naud. and its allies.

COLLECTIONS

Below are listed the specimens collected from the various populations of formicarial melastomes studied in the field; a full set of these is deposited at Kew (K), nearly complete sets at New York (NY) and at Washington (US), and a partial set at Bogotá (COL).

Maieta guianensis var. *guianensis* : Whiffin 19, 21.

Maieta guianensis var. *leticiana* : Whiffin 83 (type), 3, 22, 49, 51, 57, 60, 61, 68.

Maieta poeppigii : Whiffin 23, 24, 56, 82.

Ossaea bullifera : Whiffin 18.

Tococa juruensis : Whiffin 8.

Tococa ulei : Whiffin 4, 15, 25, 50, 62.

Tococa aff. *stephanotricha* : Whiffin 52.

For the herbarium study, further material was examined in the herbaria

of the New York Botanical Garden (NY) and of the U. S. National Museum (US).

ACKNOWLEDGEMENTS

The field observations and collections were made while a botanist on the Cambridge Medical Expedition to Colombia, 1968; I am grateful to all those who made that expedition possible (full details are given in Gundry *et al.*, 1970). The taxonomic studies were undertaken while at the New York Botanical Garden, and I am very grateful for the assistance that I received there. I am grateful also to the curators and staff of the U. S. National Herbarium (US) for allowing me to examine the collections there. I am grateful to Dr. B. L. Turner for a number of helpful comments on the manuscript, and to Mr. Geza Knipfer for preparing the illustrations. I am especially grateful to Dr. John J. Wurdack for help with the identifications, for reading the manuscript, and for his help and encouragement.

REFERENCES

- ASHTON, P. S. 1969. Speciation among tropical rain forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* 1: 155-196.
- CAIN, A. J. 1969. Speciation in tropical environments: summing up. *Biol. J. Linn. Soc.* 1: 233-236.
- FEDEROV, An. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. *J. Ecol.* 54(1): 1-11.
- GLEASON, H. A. 1931a. The relationships of certain myrmecophilous melastomes. *Bull. Torr. Bot. Club* 58: 73-85.
- . 1931b. Studies in the flora of northern South America. XV Recent collections of Melastomataceae from Peru and Amazonian Brazil. *Bull. Torr. Bot. Club* 58: 215-262.
- GUNDRY, D. R. T., *et al.* 1970. Report of the Cambridge Medical Expedition to Colombia, 1968. Published privately by the authors.
- HAFFER, J. 1969. Speciation in Amazonian forest birds. *Science* 165 (3889): 131-137.
- JANSEN, D. H. 1966. Co-evolution of mutualism between ants and acacias in Central America. *Evolution* 20: 249-275.
- . 1967. Fire, vegetation structure, and the ant x acacia interaction in Central America. *Ecology* 48(1): 26-35.
- . 1969. Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. *Ecology* 50(1): 147-153.
- MAYR, E. 1969. Bird speciation in the tropics. *Biol. J. Linn. Soc.* 1: 1-17.
- MELIN, D. 1931. Contributions to the study of the theory of selection 1. *Zool. Bidr. Uppsala* 13: 87-104.
- PIJL, L. van der. 1955. Some remarks on myrmecophytes. *Phytomorphology* 5: 190-200.
- SCHNELL, R. 1967. Contribution a l'étude des genres Guyano-Amazoniens *Tococa* Aubl. et *Maieta* Aubl. (Melastomacées) et de leurs poches foliaires. *Adansonia sér. 2*, 6(4): 525-532.
- SPRUCE, R. 1908. Notes of a botanist on the Amazon and Andes. London.
- STEENIS, C. G. G. J. van. 1969. Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution. *Biol. J. Linn. Soc.* 1: 97-133.
- WHIFFIN, T. 1970. Botany. In D. R. T. Gundry *et al.*, Report of the Cambridge Medical Expedition to Colombia, 1968.
- . 1971. Studies in the genus *Maieta* Aubl. (Melastomataceae). *Brittonia* 23: 325-329.